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Maternal influences on egg and larval characteristics of plaice (*Pleuronectes platessa* L.)

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Abstract

Maternal influences on various egg and larval characteristics were examined using plaice from the Irish Sea and Norwegian coastal waters. Thirty-nine batches of eggs were incubated during the spawning season of 2004 and 2005. Thirty-seven larvae from one batch were also monitored individually to examine the influence of egg size on larval size at hatching, yolk sac volume and growth at the individual level. The relationship between egg dry weight (EDW) and egg diameter (ED) differed between the fish from different origins. Egg size increased with maternal size and decreased with progression through spawning. Eggs from the Norwegian coast hatched on average two days earlier than eggs from the Irish Sea. This resulted in the larvae from the Norwegian coast hatching at a smaller size and with larger yolk sac volumes. Larger eggs gave rise to larvae with larger yolk sac volumes at hatching (independent of incubation period) both at the batch and individual level. Larval growth rate was influenced by larval hatching size and yolk sac volume with smaller larvae and larvae with larger yolk sacs having a greater growth rate between hatching and two weeks after hatching. The effects of egg size on larval plaice were present until the end of the yolk sac stage due to differences in the time taken to absorb the yolk sac. Neither hatching rate, age at first feeding nor larval survival was related to maternal size or egg dry weight.

Keywords: Plaice; *Pleuronectes platessa*; Maternal effects; Egg size; Larvae; Growth

1. Introduction

Current fisheries assessment models include only limited biological details for the processes occurring between spawning and recruitment. Instead they traditionally assume that total egg production (reproductive potential) and recruitment is proportional to the spawning stock biomass (SSB) (Marshall et al., 1998). However, SSB is not often an accurate measure of reproductive potential (Marshall et al., 1998; Marteinsdottir and Thorarinsson, 1998) because the reproductive potential of fish stocks varies with the age, size, spawning experience and condition of spawning fish (Marteinsdottir and Begg, 2002).

In many fish species, larger females often produce larger eggs and egg size for each female decreases with each progressive batch through spawning (Kjesbu et al., 1996; Marteinsdottir and Begg, 2002; Rideout

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et al., 2005). This has also been demonstrated in plaice (*Pleuronectes platessa*) (Rijnsdorp, 1991; Schmidt, 2001; Fox et al., 2003).

The constituents of an egg, genetic and nutritive, determines its quality since fish eggs take up little, if any, nutrients once ovulated (Brooks et al., 1997). Thus the nutritive investment in an egg must provide for the larvae through to first feeding. Egg size has been shown to be an important factor in the early life history of fish as larger eggs provide more energy for development (Hempel, 1979) and egg size is positively correlated with many larval traits including larval length at hatching (Blaxter and Hempel, 1963; Buckley et al., 1991; Rideout et al., 2005), incubation period (Dannevig, 1894; Chambers et al., 1989; Huang et al., 1999), yolk sac volume (Blaxter and Hempel, 1963; Beacham et al., 1985; Gisbert et al., 2000), first feeding age (Gisbert et al., 2000) and survival potential and resistance to starvation (Knutsen and Tilseth, 1985; Marteinsdottir and Steinarsson, 1998; Rideout et al., 2005).

Larvae with a greater size-at-age have been shown to have longer swimming endurance (Ojanguren et al., 1996) and a greater burst swimming speed both of which can help in the capture of prey items and escape from predators (Miller et al., 1988). In plaice, larger larvae have a greater escape swimming speed and are less vulnerable to planktonic invertebrate predators (Bailey and Batty, 1984).

Larger adult plaice begin spawning earlier in the season (Simpson, 1959; Rijnsdorp, 1989; Horwood, 1990), during which time the availability of food items for the hatched larvae is much lower in comparison to later in the season (Scrope-Howe and Jones, 1985). Since larger fish produce larger eggs, earlier hatched larvae may be better prepared to withstand starvation than later hatched individuals. Fishing pressure on the adult population can lead to the selective removal of larger fish thus changing the proportion of old and young spawners. To understand the implications of shifts in the structure of the spawning population it is critical to evaluate maternal influences on the characteristics of the eggs and larvae.

The aim of the present study was to examine how maternal size and the seasonal progression of spawning affects egg size, and how the egg size influences batch averages of various egg and larval characteristics. Individuals within a batch were also monitored to examine egg size influence at the individual level.

2. Materials and methods

Mature adult plaice were collected by trawl in February 2004, in the Irish Sea, from inshore areas to the east of the Isle of Man and transferred to the Port Erin Marine Laboratory (PEML). The fish were kept in circular tanks with a volume of 1800 L, 2 m diameter and a water depth of 60 cm. This had an inflow of filtered seawater at ambient temperature (6–10 °C). Each fish was measured (Total Length) and weighed and implanted with a passive integrated transponder tag (pit tag). Milt was obtained from males that were part of the broodstock of the Larval Rearing Centre in PEML.

In February 2005, mature adult plaice were obtained from local Bergen (Norway) fishermen and transported live to the Department of Biology, University of Bergen where they were kept in tanks with a volume of 500 L and dimensions $1 \times 1 \times 0.5$ (L × B × H) m with an inflow of water at 7 °C. The fish were measured, weighed and tagged. All fish were visually checked daily for signs of ovulation (high degree of swelling in abdominal area and reddening around the genital opening (Panagiotaki, 1992)). Milt was obtained from males that were caught at the same time as the females and maintained in a similar tank.

Fish that showed signs of ovulation were 'stripped' of their eggs. Egg batches that were chosen for incubation were fertilised with pooled milt, from three randomly chosen males, which was mixed with seawater then mixed in with the eggs. The eggs were then allowed to stand in a controlled temperature (CT) room at 7 °C. After 30 min, using a fine mesh hand net, the eggs were dipped in seawater to rinse off excess sperm and the entire batch was transferred to a larval rearing tank. In 2004 the larval rearing tanks consisted of black cylindrical tanks with a volume of 30 L and dimensions of 28×40 (H × D) cm with a water depth of 24 cm; these were kept in a CT room at 7 °C. The tanks had an inflow of UV sterilised filtered seawater with a mesh covered outflow at the top of the tank. The inflow of water was of ambient temperature (6–10 °C) and had a low inflow rate in order to keep the water temperature in the tank at 7 °C ± 0.5 °C. The tank also had a central air stone to circulate and aerate the water.

In 2005, the larval rearing tanks consisted of black cylindrical tanks with a volume of 15 L and dimensions of 25×32 (H × D) cm with a water depth of 19 cm. These had a gentle inflow of seawater at 7 °C ± 0.5 °C. The tanks had a mesh bottom where water flowed out to a larger holding tank. Each larval tank had a central air stone to circulate the water. All tanks were on a 10:14 hour light:dark cycle.

In all batches produced, the egg diameters of a sample of unfertilised eggs (10 in 2004, 30 in 2005) were measured to the nearest 0.01 mm using a dissecting microscope and graticule. Egg dry weight (EDW) was

measured for a sample of 50 unfertilised eggs which were rinsed with seawater, placed in a pre-weighed eppendorf type tube, dried at 60 °C, and weighed daily to the nearest 0.01 microgram until a constant weight was achieved (eggs generally reached a constant weight after 24 h). The numbers of eggs measured from the Irish Sea fish were quite low due to time restrictions and not considered to be truly representative of the batch; therefore in the analysis of larval traits EDW was used to represent the batch due to the higher number of eggs used. Throughout the rest of the text, EDW refers to the average egg dry weight for a batch of eggs and ED refers to the average egg diameter of a batch of eggs. The average EDW for a particular female was the sum of the EDW all batches produced by the female divided by the number of batches.

Unfertilised and dead fertilised eggs were removed every two days and counted. On d 12 after the eggs were spawned the numbers of surviving eggs were estimated volumetrically, this was repeated daily until the eggs hatched. When the eggs hatched the same method was used to estimate the number of larvae.

Peak hatching was defined as the period in which the largest proportion of the eggs hatched. The incubation period was defined as time between fertilisation and the morning following peak hatching (most eggs hatched during the night). The day following peak hatching was termed 1 d after hatching on which the standard length (SL) and the length and height of the yolk sac of 30 larvae were measured to the nearest 0.01 mm. The larvae were measured in 2004 using a dissecting microscope and graticule. In 2005, due to the availability of a camera and for time efficiency, the larvae were photographed under the microscope and measured using 'Image-J' image analysis software (Rasband, 1997–2005). The yolk sac was assumed to be a spheroid structure and the volume was calculated using the equation:

$$\begin{aligned} \mathrm{YSV} &= 4/3^{*}(L/2)(H/2)^{3} \\ \mathrm{YSV} &= \text{Yolk sac volume } (\mathrm{mm}^3) \\ \mathrm{L} &= \text{Length of yolk sac } (\mathrm{mm}) \\ \mathrm{H} &= \text{Height of yolk sac } (\mathrm{mm}) \end{aligned}$$

The larval length and remaining yolk sac was measured on d 6 after hatching for the Norwegian larvae which allowed the calculation of utilisation rate of yolk for these batches and the calculation of the time before the remaining yolk is exhausted (assuming a constant utilisation rate). On d 4 after hatching, food was introduced in the form of newly hatched (non-enriched) *Artemia*, which were added daily at a concentration of 500 L^{-1}. This is considered a low prey density for marine fish larvae (O'Connell and Raymond, 1970; Houde, 1975). A low prey density was used as maternal differences in eggs and larvae may only be significant under low prey densities (Rideout et al., 2005). A batch was considered to have started feeding when food was detected in the gut of larvae. This was checked at least 1 h after food was added to the tank. The percentage of larvae with food in their gut was also estimated. On d 14 after hatching, the numbers of surviving larvae were estimated, the tank was drained and the SL of 30 larvae measured as before. The specific growth (SGR) rate of the larvae was calculated using the following equation:

$$\mathrm{SGR} = ((\mathrm{Log_e}\ \text{final length} - \mathrm{Log_e}\ \text{starting length}) / \text{time in days}) \times 100$$

(Busacker et al., 1990).

Hatching rate was defined as the number of eggs that hatched as a percentage of the total number of eggs in the batch. Survival was defined as the percentage of hatched larvae that survived to two weeks after hatching.

2.1. Individuals' experiment

Forty eggs were isolated from a batch (spawned by a 43 cm female from the Norwegian experiments) on the day before peak hatching. These were photographed and placed in individual static water tanks measuring 105 × 75 × 40 (L × B × H) mm in a temperature controlled room at 7 °C. The morning after hatching, each larva was photographed under the dissecting microscope. Half the volume of water was changed every other day. Newly hatched (non-enriched) *Artemia* were introduced daily after d 4 after hatching and the age at which each larva started feeding was noted. Each larva was photographed at 7, 14 and 21 d after hatching. The larvae were transferred to a small bowl for photographing using a wide mouthed pipette and photographed. Individual egg diameter, larval SL, yolk sac length and height (from which the YSV was calculated) and larval area (excluding yolk sac) was measured, to the nearest 0.01 mm, from the images using Image-J. Larval area rather than standard length was used to examine the relationship between individual egg diameter and larval size to give better resolution due to the restricted range of individual egg diameters.

2.2. Statistical analysis

All statistical analyses were done using Statistica 6.1 (StatSoft Inc., 2002). EDW and ED were tested for normal

	fish ID	ML (cm)	MWt (g)	Batch rank													
				1	2	3	4	5	6	7	8	9	10	11	12	13	total batches
Irish Sea	5114	27	197		■												6
	E090	27	190	■													5
	9172	32	376	■													7
	F18D	32	365	■													3
	FD2D	33	360		■												6
	9A39	39	721	■			■										7
	8AAC	32	387	■	■												5
	8ACE	34	405		■	■		■									5
	9A7C	35	479	■	■	■											7
	F23A	37	630	■	■	■	■	■									5
	7AC7	35	499		■	■	■	■	■	■							8
Norwegian coast	0054	54	2205							■				■			12
	93D2	41	900							■							7
	7570	44	957				■				■						10
	F911	48	1598				■										12
	2E0F	42	884				■										8
	99D9	43	920				■	■		■	■						8
	7F02	49	1603									■		■		■	13
	FC21	45	1043					■									9

Fig. 1. Length of individual plaice (*Pleuronectes platessa*) and the total batches produced over the spawning season (indicated by grey boxes). Incubated batches are shown by black boxes. ML = maternal length MW = maternal weight.

distribution of data. The data was normally distributed and single factor regression was used to analyse the relationship between EDW and ED for the Irish Sea fish and the Norwegian coastal fish. The slopes of the regression for the two areas were compared using ANCOVA. Maternal fish weight was Log_e transformed to achieve normal distribution of data. A correlation was calculated between the mean EDW of all egg batches produced by each female and the Log_e maternal weight using single factor regression. The effect of maternal origin on EDW independent of size was tested by ANCOVA using a separate slopes model due to the sharp rise in EDW with maternal size at small sizes.

All larval traits were tested for normality with YSV, YSV on 6 d after hatching and SGR being Log_e transformed to fit the normality requirements. The

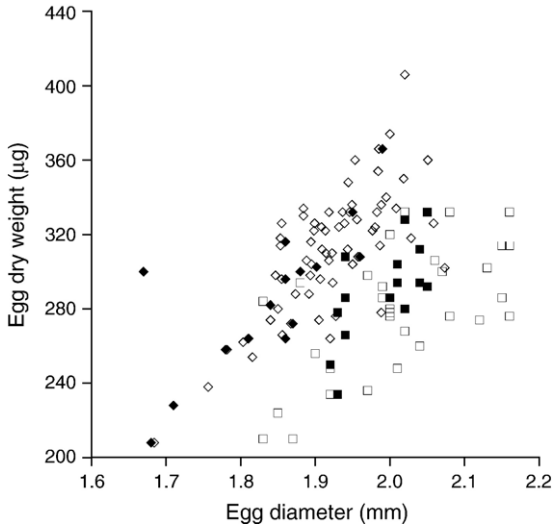

Fig. 2. Relationship between the average egg diameter (ED) and average egg dry weight (EDW) for each batch of eggs produced by the Irish Sea (□) and Norwegian coastal plaice (*Pleuronectes platessa*) (◇) (incubated egg batches are shown by filled symbols).

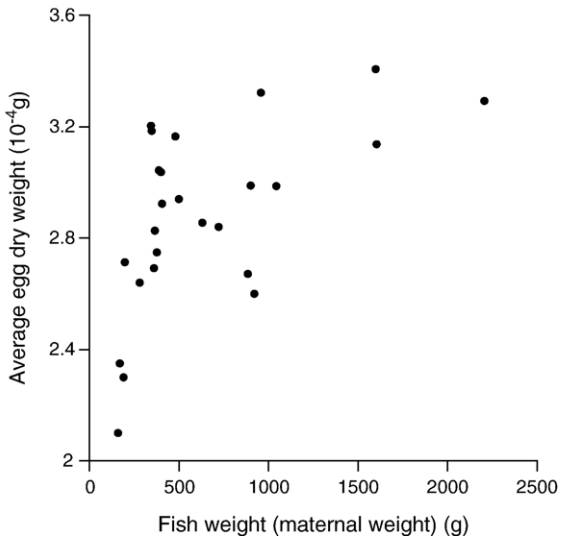

Fig. 3. Relationship between maternal weight and overall average egg dry weight (EDW), based on all egg batches produced by each individual plaice (*Pleuronectes platessa*).

Table 1
Results of ANCOVA (separate slopes model) of plaice (*Pleuronectes platessa*) maternal weight and origin (Norwegian coast and Irish Sea) on average egg dry weight of all batches

	SS	df	MS	F	p-level
Intercept	0.016319	1	0.016319	0.296828	0.591617
Weight * Origin	1.055941	2	0.527971	9.603232	0.001092
Origin	0.007342	1	0.007342	0.133543	0.718441
Error	1.154547	21	0.054978		

SS=sum of squares df=degrees of freedom MS=mean squares.

relationships among the different larval traits were investigated using a combination of principal components analysis (PCA) and ANCOVA. PCA was used to examine which factors were correlated while ANCOVA was used to investigate differences due to maternal origin with maternal origin used as a grouping variable. Homogeneity of variance was tested using Levene's test. The relationship between yolk sac volume on d 6 after hatching and EDW was analysed by single factor regression. The change in the standard deviation of larval sizes was analysed in relation to age at first feeding using single factor regression.

For the individuals' experiment, YSV was normalised by a Log_e transform. Single factor regressions were carried out on individual egg diameter and the measured larval traits at two and three weeks after hatching. The relationship between SGR and YSV and larval SL at hatching was analysed using multiple regression.

3. Results

The Irish Sea plaice began spawning on 23 February and continued until 8 April 2004. A total of 24 batches of eggs were incubated from 11 females ranging in size from 27 to 39 cm, average 29 cm. The fish from the Norwegian coastal waters spawned from 24 February until 2 April 2005. A total of 15 batches were incubated (but only 8 were raised until two weeks post hatch due to problems with experimental setup) from 8 females ranging in size from 42 to 54 cm, average 46 cm. The number of batches produced and the batch rank of the batches that were incubated for each female are shown in Fig. 1. Eggs were obtained from an additional 5 females from the Irish Sea that were only used in the analysis of EDW in relation to maternal weight.

Table 2
The minimum, maximum and mean values of the characteristics of the egg batches that were incubated from the Irish Sea plaice in 2004 and Norwegian coastal plaice in 2005

	Irish Sea			Norwegian coastal		
	Min	Max	Mean	Min	Max	Mean
Egg dry weight (μg)	234	363	295	208	366	282
Egg diameter (mm)	1.92	2.09	2.00	1.67	1.99	1.84
Larval SL at hatching (mm)	6.15	7.59	6.97	5.99	6.93	6.62
Yolk sac volume (mm^3)	0.35	2.21	0.89	0.15	2.60	1.42
SGR	0.11	1.54	0.55	0.32	1.08	0.69

SL=standard length.

Table 3
Results from the Principal Component Analysis showing the loadings of the two axes

Characteristic	Factor 1	Factor 2
Egg dry weight	**0.712**	0.131
Larval SL at hatching	**0.689**	**−0.644**
Log_e transformed yolk sac volume	0.029	**0.763**
Larval standard length on d 14	**0.835**	0.284
Incubation period	**0.666**	−0.499
Log_e transformed growth rate	0.154	**0.870**
Eigenvalue	2.390	1.856
% variance	39	31

Eigenvalues and percentage of variance are given. Significant correlations are shown in bold. SL=standard length.

3.1. Egg characteristics

EDW was positively correlated with ED; however, the slope of the relationship was significantly different for the two populations with Irish Sea fish having a lower EDW for an equivalent ED than the Norwegian coastal fish (ANCOVA; $F(1,29)=8.61$; $p<0.001$) (Fig. 2). The overall average EDW of all the batches produced by a single female was positively correlated with Log_e maternal weight (linear regression, $R^2=0.44$; $N=25$; $P<0.001$) (Fig. 3), which was a better predictor of average EDW

Table 4
Results of ANCOVA's of larval plaice (*Pleuronectes platessa*) traits showing dependent factor, number of samples (n), categorical predictor and predictor variables with respective p values (P)

Dependent factor	n	Catergorial factor	P	Predictor variables	P
SL at hatching	39	Maternal origin	0.49	EDW	0.130
				Incubation period	**0.001**
Yolk sac volume	39	Maternal origin	0.40	EDW	**0.010**
				Larval SL at hatching	**0.001**
Growth rate	34	Maternal origin	0.13	Larval SL at hatching	**0.001**
				Yolk sac volume	**0.006**
				Incubation period	**0.020**

Significant P values shown in bold. SL=standard length.

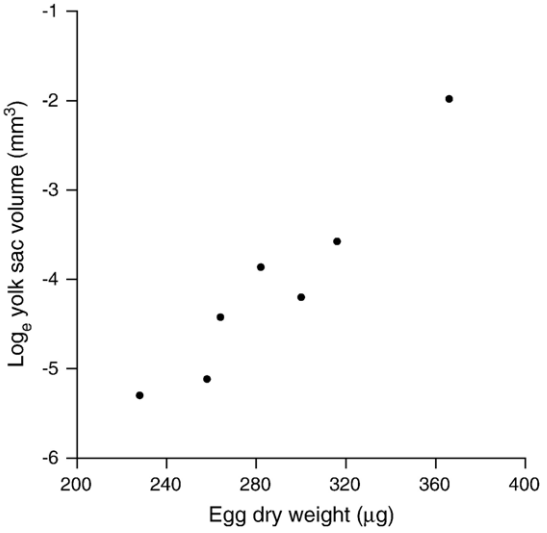

Fig. 4. Relationship between egg dry weight (EDW) and Log$_e$ yolk sac volume (YSV) remaining after 6 d post hatch in larval plaice (*Pleuronectes platessa*).

compared to maternal length. There was no effect of maternal origin, independent of maternal size, on EDW (Table 1). There was an average decrease of 12% in EDW for each individual female as the spawning season progressed, with a decrease from the first to the last batch varying from 3 to 30% between females. There was no effect of initial condition factor on egg dry weight. The magnitude of the decline in egg size did not vary significantly ($p > 0.05$) with any of the measured maternal characteristics.

3.2. Batch incubation experiment

The ranges and means for EDW, ED, larval SL at hatching, YSV and SGR (from hatch to two weeks post hatch) of the egg batches that were incubated are shown in Table 2. The incubation period varied from 13 to 17 d with an average of 16 d for eggs from Irish Sea females and 14 d for Norwegian coastal females. The hatching rate varied from 5 to 95% with an average of 48%. Survival varied from 5 to 69% with an average of 32%. Neither hatching rate nor survival was correlated with any measured maternal, egg or larval traits. The utilisation rate of yolk ranged from 0.06 to 0.42 mm^3 d^{-1} with an average of 0.26 mm^3 d^{-1} (n=7). The estimated difference in time for the utilisation of the remaining yolk by larvae from the batch with the second smallest EDW compared to the largest EDW was 14 h (utilisation rate could not be calculated for larvae from the smallest eggs as it was unknown when they had exhausted their yolk reserves). The growth rate for the first week (measured only in Norwegian fish) was higher than in the second. Larvae in the majority of batches (58%) began feeding between d 6 and 9 with larvae from only two batches feeding on d 4. The age at first feeding was not correlated with any measured larval trait.

Principal component analysis (PCA) yielded two axes explaining 39% and 31% (eigenvalues 2.390 and

Table 5
Regression summary of larval plaice (*Pleuronectes platessa*) standard length at 6 d after hatching against egg dry weight (EDW) and incubation period

	β	SE β	B	SE B	t(29)	p-level
Intercept			4.914	0.667	7.366	0.001
Egg dry weight	0.556	0.235	0.221	0.093	2.363	0.065
Incubation period	0.483	0.235	0.104	0.051	2.052	0.095

SE=standard error.

Table 6
Regression summary of larval plaice (*Pleuronectes platessa*) standard length at 14 d after hatching against egg dry weight and incubation period

	β	SE β	B	SE B	t(29)	p-level
Intercept			3.768	1.251	3.010	0.005
Egg dry weight	0.303	0.161	0.237	0.126	1.883	0.069
Incubation period	0.375	0.161	0.102	0.044	2.327	0.027

SE=standard error.

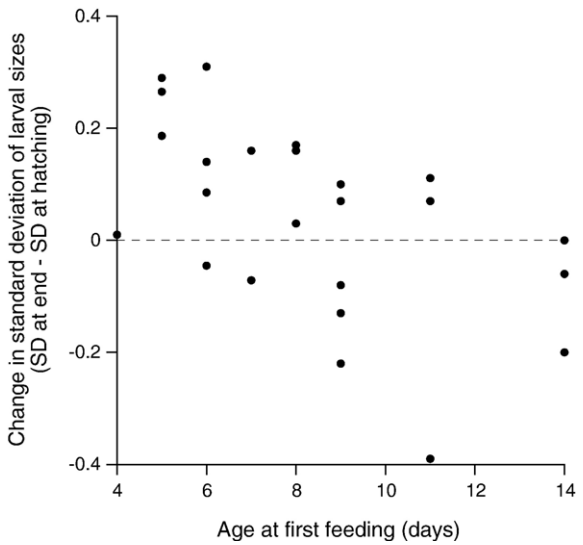

Fig. 5. Correlation between age at first feeding and the change in standard deviation of larval sizes within a batch of larval plaice (*Pleuronectes platessa*) from hatching to two weeks post hatch.

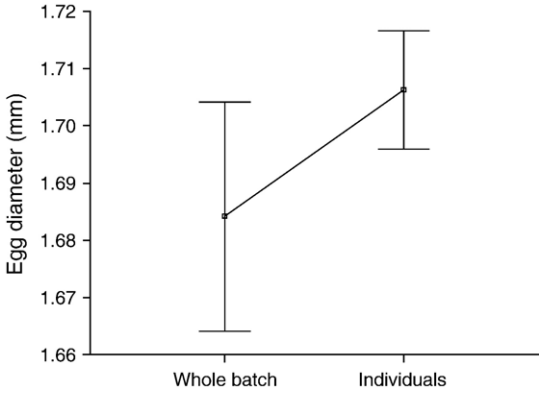

Fig. 6. Egg diameter (ED) of entire batch of plaice (*Pleuronectes platessa*) eggs before fertilisation and eggs that were used in the individual experiment (egg sizes for individuals were adjusted for increase in egg size due to development). Values shown are means± 1.96 S.E.

1.865) of variability in the data, respectively, with EDW larval SL at hatching, larval SL on d 14 and the incubation period being positively correlated on axis 1. On axis 2, yolk sac volume and growth rate were positively correlated and both were negatively correlated with larval SL at hatching (Table 3).

The results of the ANCOVAs of larval traits showed that larval SL at hatching was affected by incubation period ($p=0.001$) but not by maternal origin ($p>0.05$) or EDW ($p>0.05$). YSV was correlated with EDW ($p=0.01$) and larval SL at hatching ($p=0.02$) but was unaffected by maternal origin ($p>0.05$). Growth rate was affected by larval SL at hatching ($p<0.0001$), YSV ($p=0.006$) and incubation period ($p=0.020$) but not maternal origin ($p>0.05$) (Table 4).

The YSV (Log_e transformed) remaining at 1 week post hatch was positively correlated with EDW (linear regression; $R^2=0.91$ $N=7$ $p<0.001$) (Fig. 4). Larval SL on d 6 was correlated with a combination of EDW and incubation period (multiple regression; $F_{(2,5)}=8.61$ $P<0.05$) but neither single factor was significantly correlated with SL ($P>0.05$) (Table 5). SL on d 14 after hatching was still significantly correlated with a combination of EDW and incubation period (Multiple regression; $F_{(2,29)}=5.57$, $P<0.01$), but incubation period was now significantly correlated with SL ($P<0.05$) (Table 6). The change in standard deviation of larval sizes between hatching and 14 d after hatching was negatively correlated with age at which a batch showed signs of feeding. The standard deviation generally increased with batches that started feeding before d 9 after hatching and the standard deviation generally decreased with batches that fed after d 9 after hatching (Fig. 5).

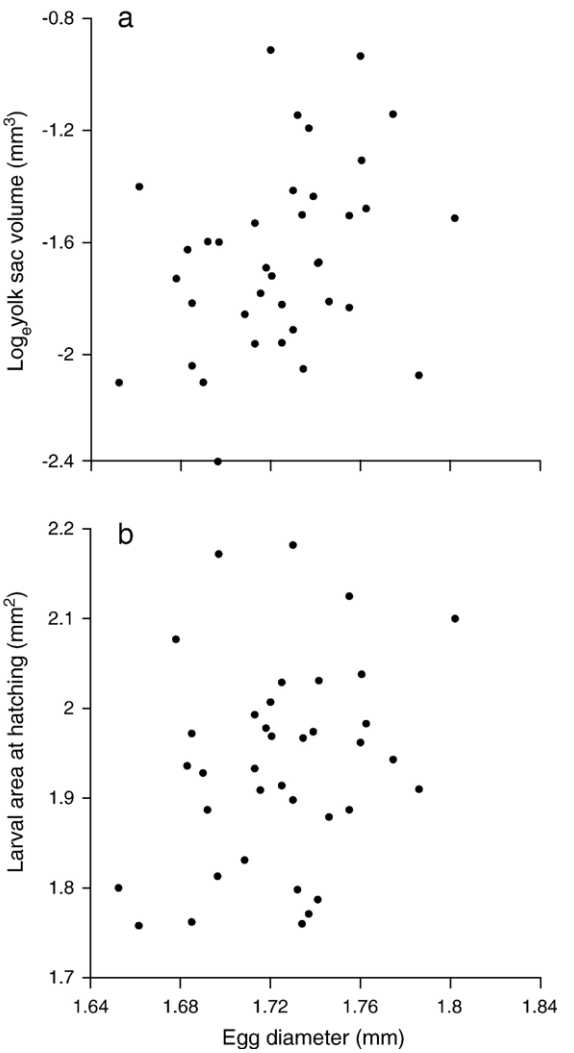

Fig. 7. Correlation between egg diameter and (a) Log_e transformed yolk sac volume, and (b) larval area at hatching for individually followed larval plaice (*Pleuronectes platessa*).

3.3. Individuals' experiment

The eggs used in the individuals' experiment ranged from 1.65 to 1.80 mm in diameter (mean±1 sd: 1.72±

Table 7
Regression summary for SGR of larval plaice (*Pleuronectes platessa*) against larval standard length at hatching (LLH) and Log_e transformed yolk sac volume (YSV)

	β	SE β	B	SE B	t(27)	p-level
Intercept			5.116	1.049	4.875	0.000
LLH	−0.542	0.131	−0.655	0.158	−4.130	0.000
YSV	0.477	0.131	0.251	0.069	3.633	0.001

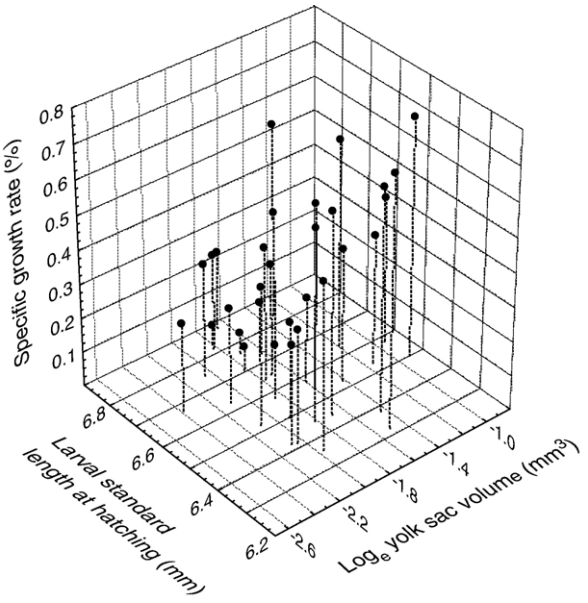

Fig. 8. Contour plot of relationship between specific growth rate, Log$_e$ transformed yolk sac volume and larval standard length at hatching for individually followed larval plaice (*Pleuronectes platessa*).

0.03). In order to back-calculate the diameter of the eggs before fertilisation the measured values were decreased by 1% in accordance with Van der Wateren et al. (1990) to account for the increase in egg size during incubation. The size range and mean of the samples of the egg diameters taken from the entire batch before fertilisation and those taken for the individuals' experiment were significantly different (t-test, $t=-2.14$; $n=70$; $p=0.04$) (Fig. 6). All eggs taken for the individual experiment hatched during the night after being transferred to individual beakers. Three larvae died after hatching. The larval SL at hatching ranged from 6.32 to 6.88 mm, larval area at hatching ranged from 1.76 to 2.18 mm^2 and YSV ranged from 0.09 to 0.40 mm^3. The SGR of larvae in the first week ranged from 0.06 to 0.73 with an average of 0.18.

Individual ED was positively correlated with individual YSV (linear regression; $R^2=0.11$; $n=37$; $p=0.04$) (Fig. 7a) and individual larval area at hatching (linear regression; $R^2=0.12$; $n=37$; $p=0.04$) (Fig. 7b). There was no significant correlation between egg diameter and larval SL at hatching (linear regression; $p>0.05$). SGR in the first week after hatching was a function of both YSV and larval SL at hatching as it was positively correlated with YSV and negatively correlated with larval SL at hatching (Table 7, Fig. 8). There was no correlation between larval SL at hatching and SGR (linear regression; $p>0.05$) or YSV and SGR (linear regression; $p>0.05$) for the period of hatch to 14 d after hatching or from 6 d after hatching to 14 d after hatching. The yolk reserves were completely used up in all larvae by the end of the first week. There was no relationship between egg diameter and larval area 6 d after hatching (linear regression; $p>0.05$).

4. Discussion

Although this experiment was conducted in two different locations, with two different plaice populations, location and origin may have had some influence, but did not obscure the main results observed. Paternal effects, which are known to be an issue in early life history studies (Trippel et al., 2005), were not controlled because it was not possible to use the same males in the Norwegian and Irish Sea study, neither was it possible to set up replicates to test for such effects. The selection of males for fertilisation was random; however, paternal effects on the eggs and larvae are a possible source of error in the results. Maternal origin is also another potential source of error, and the effect was examined. The relationship between EDW and ED and incubation period were the main differences due to maternal origin, other larval traits were unaffected by maternal origin except indirectly due to differences in the length of incubation period (discussed further below). The water temperature in the adult tanks also differed between the Norwegian and Irish Sea experiment. It is known that rearing temperature can affect egg size in some species (Hotta et al., 2001; Funamoto and Aoki, 2002). However, temperature did not appear to affect the egg sizes in the present experiment as there was no effect of maternal origin on egg size independent of maternal weight.

There was a consistent link between maternal size and egg size in these experiments, as noted previously by Fox et al. (2003). No such link was found by Rijnsdorp (1991), but this was probably because only one batch of eggs was sampled for each female. The best fit relationship was logarithmic; this was strongly influenced by the three fish with EDW below 240 μg. These are most likely to be recruit spawners (inferred from their size, see Nash et al., 2000); it has been found previously in other species that there is a large increase in EDW between recruit and repeat spawners (Hislop, 1988; Kjesbu et al., 1996) which may be due to recruit spawners having a lower amount of energy available for their first reproductive season. The relationship between maternal size and egg size has been demonstrated in many other species including brown trout (*Salmo trutta*) (Ojanguren et al., 1996), cod (*Gadus morhua*) (Marteinsdottir and Steinarsson, 1998; Trippel, 1998; Marteinsdottir and Begg, 2002), haddock

(*Melanogrammus aeglefinus*) (Trippel and Neil, 2004) and winter flounder (*Pseudopleuronectes americanus*) (Buckley et al., 1991).

As shown in previous studies (Rijnsdorp, 1991; Schmidt, 2001; Fox et al., 2003) eggs from an individual female decreased in size as spawning progressed, whether measured as ED or EDW. This has also been documented in two related species: yellowtail flounder (*Pleuronectes ferrugineus*) (Manning and Crim, 1998) and winter flounder (Buckley et al., 1991). The average decrease in EDW of 12% in the present study is similar to that found by Rijnsdorp (1991) in wild North Sea plaice and by Schmidt (2001) in captive Irish Sea plaice. Several reasons have been suggested for this decrease in egg size including temperature (Marsh, 1984; Houghton et al., 1985; Imai and Tanaka, 1987; Chambers, 1997), depletion of body reserves (Kjesbu et al., 1991; Hsiao et al., 1994; Chambers and Waiwood, 1996) or endogenously influenced hormonal profiles (Kjesbu et al., 1996). Temperature appears to have very little effect on the seasonal decline in the egg size of plaice. This is supported by the decline in egg size in the Norwegian fish, despite a constant temperature during the experiment. This is consistent with investigations on other species (Chambers and Waiwood, 1996; Trippel, 1998). Chambers and Waiwood (1996) concluded that the decline in egg size in cod was related to deteriorating female condition. Female condition was not assessed during spawning in the present study so it was not possible to link the decline in egg size to a decline in fish condition.

Initial fish condition did not have any effect on average EDW, EDW of the first batch or the magnitude of the decline in EDW through spawning. This is consistent with the results of Kjesbu et al. (1996) and Trippel (1998) for cod. However, this is in contrast to the study by Chambers and Waiwood (1996), who found that condition factor (Fulton's K) was positively correlated with egg size. The reasons for these contrasting results are unclear but it is known that plaice regulate their reproductive output in response to decreased energy reserves by reducing fecundity through atresia (Kennedy, 2006).

The reason for the difference in the relationship between EDW and ED of fish from the Irish Sea and Norwegian coast is unclear but the difference will affect the density of the eggs with the eggs produced by the Norwegian fish having a greater density. The difference may be related to maintaining the buoyancy of the eggs as different bodies of water differ in salinity and temperature, which affects water density. Eggs produced by Baltic cod are more buoyant than Atlantic cod eggs, which prevents sinking in the more brackish conditions experienced in the Baltic Sea (Nissling et al., 1994). The eggs produced by the Norwegian females hatched on average 2 d earlier than the Irish Sea eggs. Differences in egg development rates have been observed previously in plaice with eggs from the Irish Sea hatching up to 2 d earlier than eggs from the North Sea at the same temperature (Fox et al., 2003). The differences between the two groups in the present study are not thought to have affected the experiment as egg dry weight was used as an indicator of egg quality. Egg dry weight is a measure of the total constituents of the eggs whereas differences in the egg diameter may be due to differences in the hydration of the egg. The responses of the resulting larvae in respect to yolk absorption and growth appear to be due to the resulting SL at hatching due to a shorter incubation period rather than directly from different maternal origin. This has also been observed in herring (*Clupea harengus*) larvae where larvae released from eggs early had a higher increase in length than larvae that hatched naturally (Geffen, 2002).

The difference in the mean size of the eggs between those used in the individuals' experiment and of the mean egg size of the entire batch they came from (which was measured before fertilisation) could be due to size selective mortality during the incubation period or could also be due to the smaller eggs hatching first. Only one batch was used during the individuals' experiment so it is unknown if this is true for other batches. This trend was not seen in the batch experiment; however, smaller eggs have been seen to hatch earlier in flounder (*Platichthys flesus*) (Dannevig, 1894), black porgy (Acanthopagrus schlegeli) (Huang et al., 1999), dace (Leuciscus leuciscus) (Mann and Mills, 1985), and capelin (Mallotus villosus) (Chambers et al., 1988).

Larval size at hatching was not related to egg size in the batch experiment but it was positively correlated with egg size in the individuals' experiment. This inconsistency may be due to the positive correlation between SL at hatching and incubation period in the batch experiment which may obscure the relationship as the number of samples within each incubation period was small. A link between egg size and larval size at hatching has been reported in many other species including cod (Knutsen and Tilseth, 1985; Marteinsdottir and Steinarsson, 1998), haddock (Rideout et al., 2005), herring (Blaxter and Hempel, 1963), winter flounder (Buckley et al., 1991), striped bass (*Morone saxatilis*) (Monteleone and Houde, 1990), dace (Mann and Mills, 1985) and Siberian sturgeon (*Acipenser baeri*) (Gisbert et al., 2000).

There was a consistent link between egg size and YSV, both between and within batches. In the batch experiment there was an inverse relationship between larval SL at hatching and YSV which was not seen in the individuals'

experiment. This can be explained by differences in incubation periods with a difference of up to 3 d between the later and earlier hatched batches. A longer incubation period resulted in the larvae using more reserves before hatching than earlier-hatching batches and so they have a larger SL at hatching, resulting in the inverse relationship. However, in the individuals' experiment all the larvae hatched within 24 h. Therefore they would all be at a similar stage of development and so there would be no relationship between YSV and SL at hatching. The former relationship has been observed in capelin where hatching later exacted a cost on yolk reserves (Chambers et al., 1989). Age at hatching influenced larval length and yolk sac volume in herring (Geffen, 2002). An increase in YSV with egg size has been observed in other species including cod (Trippel, 1998), herring (Blaxter and Hempel, 1963), capelin (Chambers et al., 1989), brown trout (Ojanguren et al., 1996), haddock (Rideout et al., 2005), black porgy (Huang et al., 1999), and Siberian sturgeon (Gisbert et al., 2000).

SGR was influenced by larval SL at hatching and YSV, with smaller larvae with larger yolk sacs having the highest growth rate. The increase in SGR with lower SL at hatching and higher YSV was due to the larvae endogenously feeding for a greater period (larval growth was greater during endogenous feeding compared to exogenous feeding). This was evident from the SGR being lower in the second week after hatching compared to the first. The relationship between SGR, YSV and larval SL at hatching disappeared after 1 week in the individuals' experiment but was still apparent after two weeks in the batch experiment. This was probably the result of the larvae in the individuals' experiment having a very low YSV at hatching (in comparison with the averages of the batches in the batch experiment which is probably due to the very low EDW of the batch they came from) so that they had used up their yolk sac reserves by the end of the first week. The yolk sac reserves of the larvae in the batch experiment persisted for a longer period so the relationship between larval SL at hatching and SGR was still evident at the end of the second week.

Smaller larvae had a greater SGR because they have a lower respiration rate, which rises isometrically with body weight in larval fishes (Giguere et al., 1988; Nelson and Wilkins, 1994). This implies that to meet metabolic needs, larger larvae need more food (Giguere et al., 1988). Therefore smaller larvae would utilise their yolk reserves at a slower rate than larger larvae, thus extending endogenous feeding for a longer period of time resulting in a higher SGR. This was seen by Panagiotaki (1992), where smaller, earlier-hatched larvae had a lower mean daily yolk sac utilisation rate than their larger, later-hatched siblings.

There was no relationship between larval length on d 6 or 14 after hatching. The relationships between EDW and larval SL on d 6 or 14 show positive but not significant trends. The main influence on larval SL on d 14 was incubation period, but this was not the case for larval SL at d 6 though the sample size was small ($N=8$). Egg size no longer had an influence on larval size after one week in the individuals' experiment. In the batch experiment larvae from eggs with a greater EDW had a greater amount of yolk reserves remaining 6 d after hatching. This means that larvae from larger eggs have more time to find food before the 'point of no return' (Ehrlich, 1974). In zebrafish (*Danio rerio*), where the yolk sac volume was manipulated experimentally, yolk sac volume was positively correlated with the time to yolk sac absorption and larval size at complete yolk sac absorption (Jardine and Litvak, 2003). Yolk manipulation from herring embryos resulted in decreased larval length at hatching, especially for smaller sized eggs (Morley et al., 1999).

From the current study it can inferred that egg size exerts an influence on plaice larvae through to the end of the yolk sac stage by influencing the duration of the yolk sac stage. The influence of egg size on larval size may have been obscured in the current experiment because the incubation period differed between batches and the larvae in different batches commenced feeding at different ages. The effects of egg size on larval SL persists for differing times in different species; Glebe et al. (1979), working with Atlantic salmon, *Salmo salar*, reported that the length of the fry was still correlated with original egg diameter some eight months later. Wallace and Aasjord (1984) found that the effect of egg size on the length of Arctic charr (*Salvelinus alpinus*) alevins was still clearly evident after 140 d post hatch. The maternal influence on larval size of striped bass was still evident after 25 d post hatch (Monteleone and Houde, 1990). Larval size still remained correlated with egg size in tilapia (*Oreochromis massambicus*) after 22 d post hatch (Rana, 1985) and the effect of egg size on Siberian sturgeon larval size was still evident at 20 d post hatch (Gisbert et al., 2000).

The change in standard deviations of larval SL is related to age at first feeding. There was a decrease in standard deviation of larval sizes within a batch if the larvae did not feed until after approximately 9 d post hatch and an increase if the larvae started before 9 d post hatch. The decrease in standard deviation within a batch of larvae not feeding before 9 d could be due to smaller larvae 'catching up' with their larger siblings. This has been noted previously by Panagiotaki (1992), who showed there was a decrease in size variation of plaice

larvae between hatching and the end of the yolk sac stage when no food was offered. The decrease in the present study could also be due to size selective mortality.

4.1. Implications for larvae

There was no link between any of the measured maternal, egg or larval traits on survival of the larvae from hatch to two weeks after hatching. No link has been found in other species kept under high prey densities (McEvoy and McEvoy, 1991; Gisbert et al., 2000; Jonsson and Svavarsson, 2000; Rideout et al., 2005); however; the prey density in the present study was low (O'Connell and Raymond, 1970; Houde, 1975). Larger plaice invest greater amounts into each individual larva. This infers there are advantages to hatching with greater amount of reserves which were not apparent in the present study. Having a greater amount of yolk reserve will allow a larva to live by endogenous feeding for a longer period so have a greater amount of time to find food. The remaining yolk sac volume after 6 d was only measured for a small number of larvae so the results did not allow a calculation of a general utilisation rate of yolk for plaice larvae. However, the difference in the amount of yolk left after 6 d for larvae from the second smallest and largest eggs shows that larvae from the largest eggs could survive by endogenous feeding for approximately another 14 h. The period of endogenous feeding between the largest and smallest eggs is likely to be longer; however, this could not be estimated as it was unknown when the larvae from the smallest eggs had exhausted their yolk. With greater amounts of yolk the larvae should have a greater chance of finding food before starvation, therefore, larvae from larger females which spawn earlier in the season than smaller females (Rijnsdorp, 1989), and the larvae from early season batches, both of which have a greater EDW, are more able to deal with the low zooplankton density at the beginning of the season (Scrope-Howe and Jones, 1985) than larvae from later batches and smaller fish.

5. Conclusion

Larger female plaice produce eggs with a greater egg dry weight which result in larvae with a greater yolk sac volume. Eggs produced by plaice from the Norwegian coast hatch on average 2 d earlier than eggs from the Irish Sea. This leads to larvae from the Norwegian coast hatching at a smaller size but with a greater yolk sac volume. In the current study, the main influence of egg size on the resulting larvae was through the size of the yolk sac. Egg size was correlated with larval size at hatching in the individuals' experiment but this correlation was not present across batches. Growth in the first two weeks after hatching was dependent on size at hatching and the volume of the yolk sac. The effects of egg size on larval plaice were present until the end of the yolk sac stage due to differences in the time taken to absorb the yolk sac. This will allow larvae from larger eggs to find food before starvation. Larvae from larger eggs had no survival advantage over larvae from smaller eggs under the present experimental conditions.

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